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Synchronisation of an excitatory integrate-and-fire neural network

Grégory Dumont Jacques Henry

Abstract

In this paper we study the influence of the coupling strength on the synchronization behavior of a population of leaky integrate-and-fire neurons that is self excitatory with a population density approach. Each neuron of the population is assumed to be stochastically driven by an independent Poisson spike train and the synaptic interaction between neurons is modeled by a potential jump at the reception of an action potential. Neglecting the synaptic delay we will establish that for a strong enough connectivity between neurons, the solution of the partial differential equation which describes the population density function must blow up in finite time. Furthermore, we will give a mathematical estimate on the average connection per neuron to ensure the occurrence of a burst. Interpreting the blow up of the solution as the presence of a Dirac mass in the firing rate of the population, we will relate the blow up of the solution to the occurrence of the synchronisation of neurons. Fully stochastic simulations of a finite size network of leaky integrate-and-fire neurons are performed to illustrate our theoretical results.

1 Introduction

Synchronous activity of a neural network is ubiquitous in the brain. These neural oscillations reflect the synchronized discharge of a large number of neurons. Such synchronous activity can be detected for example, by measuring the local field potential. Recent experiments in neurobiology have renewed interest in the cooperative dynamical properties of large neuronal systems, in particular, the emergence of synchronized patterns of neural activity and their computational role. Synchronized firing has been observed among cultured cortical neurons and it is believed that it serves a prominent role in information processing functions of both sensory and motor systems. However, synchronization is not always desirable. For example, synchronization of individual neurons leads to the emergence of pathological rhythmic brain activity in Parkinson's disease, essential tremor, and epilepsies.

There are lots of investigations regarding the synchronization of a neural network. Many works have been done to explain the occurrences of oscillations, most of them using a mean field approach and rate models with the first step

made in [Wilson and Cowan, 1972]. Another important result has been established in [Amari, 1977] with the so-called neural field approach, where the spatial distribution of the neural network is taken into account and pattern formation may be observed. A recent review of the neural field method is presented in [Bressloff, 2012], see also [Ermentrout and Terman, 2010] and [Bressloff, 2009] for a brief introduction. Another approach consists in seeing an individual cell of the network as an oscillator. The reader can find some mathematical tools in [Kopell and Ermentrout, 2000] to investigate synchronisation with this point of view (see also [Ermentrout and Terman, 2010] and [Bressloff, 2009] for an introduction to these researches). Also one can find a deep investigation of the occurrence of synchronization with a population density approach for integrate-and-fire neurons with inhibitory connections in [Fourcaud and Brunel, 2002], [Ostojic et al., 2009], [Brunel and Hakim, 1999] and [Brunel, 2000]. It has been proved that a Hopf bifurcation might occur, and thus periodical solutions can be observed for a certain range of parameter.

In this paper we consider a fully stochastic network of leaky integrate-and-fire neurons with an excitatory all-to-all coupling. Each neuron of the population is assumed to be driven by an independent Poisson spike train coming from an external source. If a neuron receives an action potential its membrane potential makes a small jump. When a neuron fires and emits an action potential, each other neuron of the network may be affected. Nonetheless, we will assume that on average each action potential reaches J other neurons. In other words, J may be seen as the average number of connections per neuron. It is well known (see [Omurtag et al., 2000] for example) that assuming the population has an infinite number of neurons it is possible to derive a nonlinear partial differential equation (PDE) for the evolution of its density function $p(t, v)$ at time t and potential v and the corresponding population firing rate $r(t)$.

The well posedness of the nonlinear PDE of the population density model for self excitatory or inhibitory populations was recently studied in [Dumont and Henry, 2012]. For a population of self-excitatory neurons without conduction delay the well posedness was only obtained for a weakly coupled populations (i.e. for a weak average connection per neuron). In this paper we will study populations with a stronger coupling and we will discuss the local existence of a solution of the PDE. The necessary mathematical ideas to prove this result are close to the mathematical ideas already proposed in [Dumont and Henry, 2012], for this reason we will only sketch its proof.

To explain and predict the synchronization, we adopt in this article the point of view of the recent works done in [DeVille and Peskin, 2008], [DeVille et al., 2010] and [Cáceres et al., 2011] where the blow up of the firing rate $r(t)$ is studied. We will prove that for a high average number of connection per neuron the solution of the PDE must blow up. Indeed the main result of this paper is that:

- *Considering an excitatory network of leaky integrate-and-fire neurons stochastically driven by an independent Poisson spike train, if the average connection per neuron J is too strong, then the firing rate of the network $r(t)$ reaches infinity in finite time.*

We will relate the blow up of the activity to the occurrence of a Dirac mass in the firing rate due to the fact that a part of the population fires at the same time. This interpretation will be confirmed by the simulation of a finite size network of leaky integrate-and-fire neurons.

The paper is organised as follow. The first part deals with the derivation of the partial differential equation which models a population of leaky integrate-and-fire neurons. The second part is dedicated to the mathematical study of the model and is separated in two sections. In the first section, we study the simplest case of a population of non leaky integrate-and-fire neurons. This case can be reduced to a non linear dynamical system that has already been studied in [DeVille et al., 2010]. After recalling their results regarding the trend of such populations to synchronise, we study the general case of a population of leaky integrate and fire neurons. We discuss the well posedness and the blow up of the solution in finite time. Following the same ideas as in [DeVille et al., 2010], we relate the blow up with the synchronisation property of the neural network and give a mathematical criterion for the occurrence of a burst. In the last section, to illustrate our main mathematical result, we show some numerical simulations of a finite size excitatory network of leaky integrate-and-fire neurons where the synchronization can be observed. We finally give a conclusion and some directions for future investigations.

2 The model

Let us first recall the derivation of the partial differential equation used to model large populations of integrate-and-fire neurons structured by their potential as in [Omurtag et al., 2000]. The integrate and fire model is an ordinary differential equation describing the subthreshold dynamics of a single neuron and its firing. This ordinary differential equation, (see [Izhikevich, 2007] for instance), represents the state of a (normalized) leaky capacitor receiving charge impulses and is given by

$$\begin{cases} \frac{d}{dt}v(t) = -\gamma v(t) + h \sum_{j=0}^{+\infty} \delta(t - t_j) \\ \text{If } v > 1 \text{ then } v = v_r, \end{cases} \quad (1)$$

where $v(t)$ represents the potential of the neuron at time t (normalized to the interval $[0, 1]$). The t_j are the arrival times of external impulses and $\gamma > 0$ is the leakage coefficient. Here we model the effect of the reception of a spike at a synapse of the neuron by a jump of size h , ($h > 0$) of the potential v . When v crosses the threshold, here normalized to 1, the neuron fires emitting a spike and is instantly reset to v_r , the reset potential with $0 < v_r < 1$ (see [Brunel and van Rossum, 2007] for a biological motivation and [Burkitt, 2006] for a large mathematical review of this model and also [Izhikevich, 2007] for other spiking models similar to (1).

Assuming that all the neurons of the population are identical, we can derive from (1) a partial differential equation which gives the evolution in time of the population density of neurons $p(t, v)$ at potential v and at time t in

the limit of an infinite number of neurons. We assume there is no synaptic delay that is a spike emitted from a neuron provokes an instantaneous potential jump to its downstream neurons. The equation for the density is a conservation law (see [Nykamp and Tranchina, 2000], [Gerstner and Kistler, 2002], [Omurtag et al., 2000] and [Cai et al., 2006] for instance) taking into account three phenomena modelled by: a drift term due to the continuous evolution in the LIF model, a potential jump for the part of the population receiving excitatory impulses, a term due to the reset to v_r of firing neurons. Let $\sigma(t)$ denote the arrival rate of impulses and $r(t)$ the firing rate of the population. The dynamics of the density $p(t, v)$ follows

$$\frac{\partial}{\partial t} p(t, v) - \overbrace{\gamma \frac{\partial}{\partial v} (vp(t, v))}^{\text{Integrate-and-fire}} + \overbrace{\sigma(t) (p(t, v) - p(t, v - h))}^{\text{Excitation}} = \overbrace{\delta(v - v_r) r(t)}^{\text{Reset}}. \quad (2)$$

Because no neuron can enter the domain except at the reset potential, we impose the drift flux to be zero at the threshold

$$p(t, 1) = 0.$$

The firing rate $r(t)$ is the rate of neurons crossing the threshold (see Figure 1) and it is given by

$$r(t) = \sigma(t) \int_{1-h}^1 p(t, w) dw. \quad (3)$$

Using the boundary condition and the expression of $r(t)$ given by (3), one can check easily the conservation property of the equation (2) by integrating it on the interval $(0, 1)$, so that if the initial condition satisfies

$$\int_0^1 p_0(v) dv = 1, \quad (4)$$

the solution of (2) satisfies the normalisation condition

$$\int_0^1 p(t, w) dw = 1. \quad (5)$$

The impulse arrival rate $\sigma(t)$ is the sum of the external impulses $\sigma_0(t)$ arriving from another population of neurons, and the impulses caused by the population itself $r(t)$ which is supposed to be self excitatory. Denoting J the average connections per neuron, we have (see Figure 2) that $\sigma(t)$ is given by

$$\sigma(t) := \sigma_0(t) + Jr(t). \quad (6)$$

We finally give the model in its complete form

$$\begin{cases} \frac{\partial}{\partial t} p(t, v) - \gamma \frac{\partial}{\partial v} (vp(t, v)) = \sigma(t) (p(t, v - h) - p(t, v)) + \delta(v - v_r) r(t) \\ \sigma(t) := \sigma_0(t) + Jr(t) \\ r(t) = \sigma(t) \int_{1-h}^1 p(t, w) dw \\ p(t, 1) = 0 \\ p(0, \cdot) = p_0 \in L_+^1(0, 1). \end{cases} \quad (7)$$

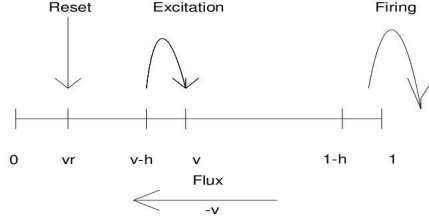


Figure 1: The evolution of the density $p(t, v)$ at potential v is due to a drift term and to jumps from $v - h$. Due to the excitation the neuron can cross the threshold, here normalized to 1, and is reset to the potential v_r .

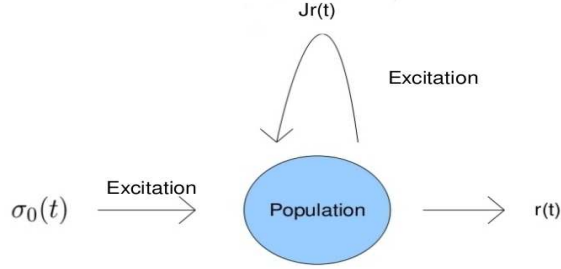


Figure 2: Scheme of a population under an external influence without conduction delay. The population receives a known external influence $\sigma_0(t)$, and produces an activity $r(t)$, also called firing rate of the population. The feedback is given by $Jr(t)$, where J is the average connections per neuron.

Before going into the study of Problem (7), let us recall that, assuming the size of the potential jump h is small, the model is often simplified by the use of an approximation of the non local term $p(t, v - h)$ by a second order Taylor expansion. Doing such an approximation, one can transform Problem (7) in a nonlinear advection diffusion problem and arrive to a model similar to the so-called non linear noisy integrate-and-fire model. This model has been successfully used for the study of inhibitory populations of integrate-and-fire neurons in [Brunel and Hakim, 1999] and both excitatory and inhibitory in [Brunel, 2000] (see also [Cáceres et al., 2011] for mathematical results with the diffusion approximation).

3 Study of the model

3.1 Non leaky integrate-and-fire

In this section we focus on the particular case when the leakage coefficient γ is taken to be zero. We arrive to a simpler model that can be reduced to a nonlinear ordinary differential system. It turns out that this dynamical system is similar to the one recently introduced in [DeVille and Peskin, 2008] and [DeVille et al., 2010] to explain the synchronisation of an excitatory neural network. We recall their results and give the critical value of the coupling parameter J to ensure the synchronisation of the neural network. Taking γ to be zero, Problem (7) reads

$$\begin{cases} \frac{\partial}{\partial t} p(t, v) = \sigma(t) (p(t, v - h) - p(t, v)) + \delta(v - v_r) r(t) \\ \sigma(t) := \sigma_0(t) + Jhr(t) \\ r(t) = \sigma(t) \int_{1-h}^1 p(t, w) dw \\ p(0, \cdot) = p_0 \in L_+^1(0, 1). \end{cases} \quad (8)$$

Let us first notice that the values of p on the interval $(0, v_r)$ are not really significant. Indeed, due to the jump process, all neurons present initially in this interval $(0, v_r)$ leave and never come back to this part of the domain. Then after a transitory dynamics, the density of neurons with a potential in $(0, v_r)$ will vanish. For the sake of simplicity, we can assume that the initial condition is actually zero on the interval $(0, v_r)$ and then forget the transitory dynamics. Let us discretize the domain into subintervals of size h . We introduce the notation

$$D_{n-k+1}(t) = \int_{1-kh}^{1-(k-1)h} p(t, w) dw, \quad k = 1, \dots, n, \quad (9)$$

where n is the number of intervals (number of compartments) of size h starting from 1 and including v_r we have

$$n = E\left(\frac{1 - v_r}{h}\right) + 1, \quad (10)$$

with $E(x)$ is the integer part of x . Since D_k is obtained by integrating the density of neurons on a subinterval, its physical meaning is clear: D_k is the number of neurons present in the compartment number k . Integrating successively the equation (8) on each subinterval, one gets a relation between the D_k . A direct computation gives

$$\begin{cases} \frac{d}{dt} D_k(t) = \sigma(t) (D_{k-1}(t) - D_k(t)) \quad \forall k = 2, \dots, n \\ \frac{d}{dt} D_1(t) = r(t) - \sigma(t) D_1(t) \\ D(0) = (D_1(0), D_2(0), \dots, D_n(0)) = D^0, \\ \sigma(t) := \sigma_0(t) + Jr(t) \\ r(t) = \sigma(t) D_n(t). \end{cases} \quad (11)$$

Let us notice that the conservation property of Problem (7) reads

$$\frac{d}{dt} \sum_{k=1}^n D_k(t) = 0, \quad (12)$$

and by the choice of normalisation

$$\sum_{k=1}^n D_k(t) = 1. \quad (13)$$

From (11), the firing rate of the population $r(t)$ can be computed and one can easily check that it is given by

$$r(t) = \frac{\sigma_0(t)D_n(t)}{1 - JD_n(t)}.$$

It is clear that this expression may become singular. We thus need to introduce a set of admissible solution for System (11). Let us set

$$X := \left\{ D = (D_1, \dots, D_n), \quad \sum_{k=1}^n D_k = 1 \quad / \quad JD_n < 1 \right\}.$$

The admissible domain X imposes a bound on the proportion of neurons in the n th compartment where are the neurons that are close to fire.

This admissible domain raises now some questions regarding System (11). The first one is about the mathematical meaning and the existence of a solution for the differential System (11). If we take an initial condition in the set X , can we find, at least for a short time, a solution to the problem? If we succeed in proving a local mathematical well posedness, can we find a criterion for the global existence? It seems from some simulations (see Figure 3) that we may observe convergence toward a stationary state. Can we determine it and study its stability? What is the physical meaning of the stationary state regarding the neural network? If we do not have global existence, can we determine a criterion to ensure the blow up in finite time? And finally, if there is a blow up, what is its physical meaning regarding the neural network?

Answers to these questions have been given in [DeVille and Peskin, 2008] and [DeVille et al., 2010], we recall the first mathematical result in the following proposition.

Proposition 1 *For all initial condition D^0 taken in the set X , there exist a time $T > 0$ and a solution D in $C((0, T), X)$ to System (11). If $J < 1$, there is a global solution, if $J > n$, there is a blow up in finite time.*

Before discussing the biological meaning of the blow up let us recall the result concerning the stationary state. We remind the reader of the following result that can be found in [DeVille and Peskin, 2008] and [DeVille et al., 2010].

Proposition 2 *Assuming that $J < n$ there exists an unique stationary state $(\bar{D}, \bar{\sigma})$ to System (11) and it is given by*

$$\begin{aligned}\bar{D} &= \left(\frac{1}{n}, \frac{1}{n}, \dots, \frac{1}{n}\right) \\ \bar{\sigma} &= \frac{n\sigma_0}{n-J},\end{aligned}\tag{14}$$

furthermore the stationary state is stable.

The proof of this result is direct. We can explicitly compute the eigenvalues λ_k of the linearized system as it is done in [DeVille and Peskin, 2008] and [DeVille et al., 2010]

$$\lambda_k = \bar{\sigma}(e^{\frac{2i\pi k}{n}} - 1) \quad k = 1, \dots, n.\tag{15}$$

Since all the λ_k are such that $\Re(\lambda_k) \leq 0$, one gets the stability result.

Let us insist that if the stationary state \bar{D} does not depend on the external activity σ_0 , nonetheless the stationary activity produced by the population itself does. Actually the stationary firing rate \bar{r} of the population can be computed from Proposition 2 and it is given by

$$\bar{r} = \frac{\bar{\sigma}}{n} = \frac{\sigma_0}{n-J},\tag{16}$$

which has a mathematical and physical meaning when $J < n$ as it is assumed in the proposition.

We show in Figure 3 a simulation of the nonlinear dynamical System (11). A gaussian function truncated to the interval $(0, 1)$ and discretized on the grid was taken for the initial condition p_0 and the external influence σ_0 was supposed constant. As we can see in the Figure 3 the solution of the dynamical system converges toward a stationary state where all compartments have the same number of neurons. We show in the last plot the evolution in time of the activity of the population $r(t)$ which oscillates before reaching its stationary value.

We present in Figure 4 some numerical results that illustrate the consequences of Proposition 1 and Proposition 2. We show the evolution in time of the activity of the population $r(t)$ for different values of the average number of connections J . In the first and the second plot of Figure 4 the activity converges toward the unique stable stationary state, which means that all the neurons of the population fire in an asynchronous way, with an activity \bar{r} given by (16). In the third plot of Figure 4 the firing rate blows up and the simulation breaks down. As it has been proposed in [DeVille et al., 2010], we can relate the blow up of the activity to the occurrence of a Dirac mass in the firing rate, which means that a part of the population fires at the same instant. We refer the reader to [DeVille and Peskin, 2008] and [DeVille et al., 2010] where simulations of fully stochastic non leaky integrate-and-fire neurons have been done. In

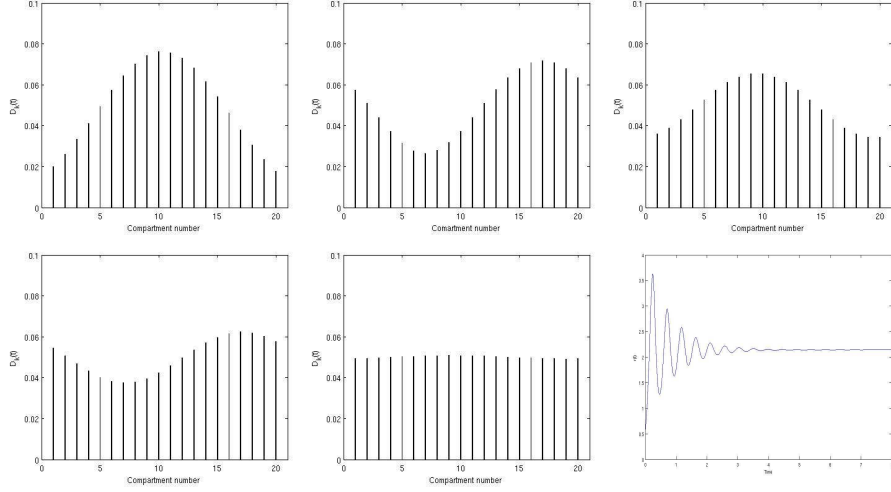


Figure 3: Simulation of the nonlinear System (11). A gaussian was taken as initial condition D^0 , the external influence $\sigma_0(t)$ was taken constant $\sigma_0 = 30$, number of compartments $n = 20$, coupling parameter $J = 5$. The five first plots show the evolution in time of the solution of System (11) at $t = 0$, $t = 0.1$, $t = 0.5$, $t = 0.7$, $t = 7$, the last one shows the activity of the population $r(t)$.

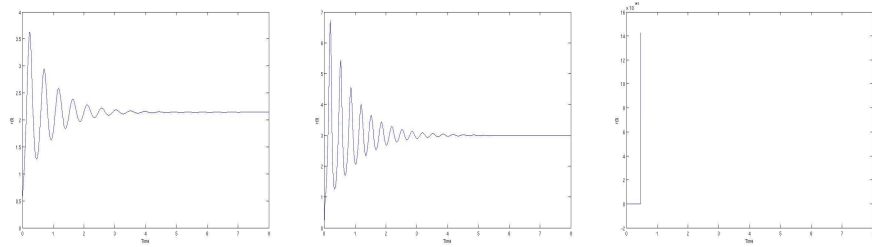


Figure 4: Simulation of the nonlinear System (11). In all plots, we show the evolution in time of the activity of the population $r(t)$. A gaussian was taken as initial condition p_0 , the external influence $\sigma_0(t)$ was taken constant $\sigma_0 = 30$, the number of compartments $n = 20$. In the first plot, the coupling parameter $J = 5$, in the second one $J = 10$, in the third one $J = 20$. We can see that the activity of the population converges to an equilibrium in the first two plots, and blows up to infinity in the third plot.

the last part of the paper simulations of populations of leaky integrate-and-fire neurons will be presented.

Let us recall the biological meaning of all these mathematical results established in [DeVille and Peskin, 2008] and [DeVille et al., 2010]. Indeed the stability of the stationary state as well as the blow up in finite time of the solution can be put in relation with the synchronisation and the desynchronisation properties of the neural network. Interpreting the stationary state as the asynchronous state of the neural network (incoherent firing response), its stability informs us that the network will always tend to desynchronise. When the average connections per neuron J is strictly smaller than 1, no blow up may happen, and the firing rate will reach its steady state. When the neural network is strongly connected (J bigger than n), there is no stationary state, the system explodes, and this phenomenon might be interpreted as an apparition of a Dirac mass in the firing rate (see the third plot of Figure 4 where the activity blows up to infinity). But when J is in the interval $(1, n)$, one can find an initial **condition** that will never lead to a blow up (such as the steady state), and it is conjectured in [DeVille et al., 2010] that there exist some initial conditions that will lead to a blow up.

In the paper [DeVille et al., 2010], the authors give a mathematical description of the burst and its consequences on the dynamics of the solution D . To do so, they introduce a map that creates a discontinuity in the dynamics of D . Such mapping permits to restart the flow of the solution D after the explosion of the dynamical system. We will not discuss this mapping since it is difficult to generalise for a LIF population described by the model (7).

3.2 Leaky integrate-and-fire

In this section, let us come back to the general Problem (7). We present in Figure 5 some simulations where all the mechanisms of the equation take place. They show the evolution in time of the potential distribution of the neuron population. In all the plots, the blue curve corresponds to a finite volume scheme discretisation of (7), (see [Omurtag et al., 2000], [Nykamp and Tranchina, 2000] and [de Kamps, 2003] for the numerical schemes and comparison with Monte Carlo simulation of the model). The first plot, upper left of Figure 5, shows the initial condition p_0 which is a gaussian. Under the influence of the external impulses $\sigma_0(t)$, taken constant in the simulation, the density function p becomes positive near the threshold value, between $1 - h$ and 1. Then a positive quantity of neurons gets out of the domain and is reset to v_r the reset potential (see Figure 1). This effect can be seen in the second plot (upper middle) of Figure 5, where a bump is present at v_r . Due to the jump process, we can see in the third plot (upper right) of Figure 5 that this bump propagates to $v_r + h$, $v_r + 2h$ and so on ... Finally the solution tends to stabilise to a steady state which can be seen in the fifth graphic (lower middle) of Figure 5. We finally show, in the last lower right plot of Figure 5 the activity of the population given by (3). In [Sirovich et al., 2006] one can find other behaviours of (7).

One can notice from (7) that the firing rate of the population $r(t)$ may be

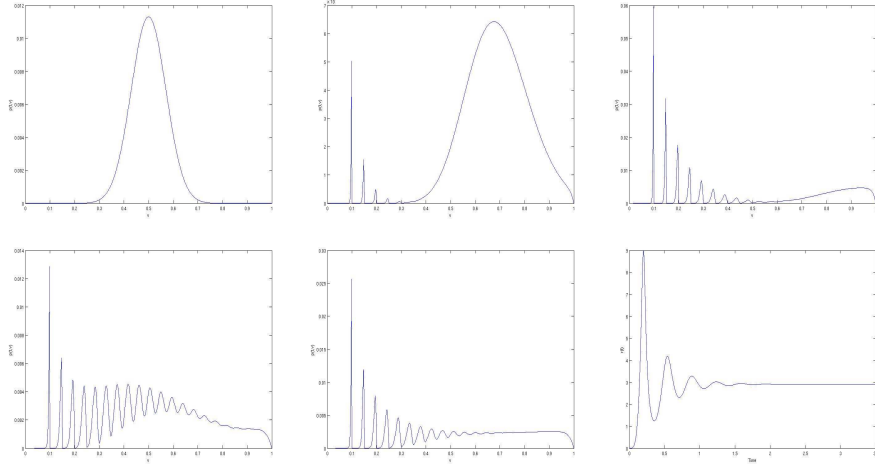


Figure 5: Simulation of the nonlinear PDE (7). A gaussian was taken as initial condition p_0 , the external influence $\sigma_0(t)$ was taken constant $\sigma_0 = 50$, the leakage coefficient $\gamma = 1$, the potential jump size $h = 0.05$, the reset potential $v_r = 0.1$, the coupling parameter $J = 5$. The five first plots show the evolution in time of the solution of PDE (7) at $t = 0$, $t = 0.1$, $t = 0.5$, $t = 0.6$, $t = 3$, the last plot shows the evolution in time of the activity of the population.

computed and it is given by

$$r(t) = \frac{\sigma_0(t) \int_{1-h}^1 p(t, w) dw}{1 - J \int_{1-h}^1 p(t, w) dw}. \quad (17)$$

The expression of the firing rate appears as a quotient that can become singular, and even be negative. Due to its physical meaning it cannot have a negative value. To avoid such difficulties, we follow the same idea as for the population of non leaky integrate-and-fire neurons, introducing a set of admissible states for Problem (7). We define

$$X = \left\{ p \in L_+^1(0, 1), \quad \int_0^1 p(x) dx = 1 \quad / \quad J \int_{1-h}^1 p(x) dx < 1 \right\}.$$

It is also the set of admissible initial condition. From the biological point of view, X is the domain of population densities with a bounded number of neurons near the threshold.

Problem (7) raises some similar mathematical questions to the ones studied for System (11). We then have to clarify the local and global existence of a solution, the existence of a stationary state, and study the stability of the stationary state. Furthermore, if we do not have global existence, we need to determine a criterion to ensure the blow up of the solution.

Let us recall that we already know from [Dumont and Henry, 2012] the following result

Theorem 3 *For all $\sigma_0 \in C(\mathbb{R}_+, \mathbb{R}_+)$ and for all $J < 1$, there exists a unique positive solution $p \in C(\mathbb{R}_+, L_+^1(0, 1))$ to Problem (7). Furthermore the firing rate r given by (3) remains bounded on \mathbb{R}_+ and we have*

$$r(t) \leq \frac{\|\sigma_0\|_\infty}{1 - J}.$$

In other words, if the average connection per neuron J is smaller than 1, the solution exists at any time, which means that the solution stays in the domain X all the time. The case $J < 1$ corresponds to a population of neurons where one neuron is connected on average to less than one upstream neuron. The network would be likely to have (large numbers of) isolated neurons. Such neurons can receive action potentials from other populations but not from the considered one. Now let us discuss the local existence for arbitrary parameters.

Theorem 4 *For all continuous and bounded σ_0 , for all $J \geq 0$, and for all initial conditions p_0 belonging to X , one can find $T > 0$ such that there exists a unique positive solution $p \in X$ to Problem (7) and $p \in C((0, T), L_+^1(0, 1))$.*

Proof To show Theorem 4, we introduce a mollified version of Problem (7)

$$\begin{cases} \frac{\partial}{\partial t} p(t, v) - \gamma \frac{\partial}{\partial v} (vp(t, v)) + S_\epsilon[\sigma](t) (p(t, v) - p(t, v - h)) = \delta(v - v_r) r(t) \\ S_\epsilon[\sigma](t) := \frac{\sigma_0(t)}{\max(\epsilon, 1 - J \int_{1-h}^1 p(t, w) dw)} \\ r(t) = S_\epsilon[\sigma](t) \int_{1-h}^1 p(t, w) dw \\ p(t, 1) = 0 \\ p(0, \cdot) = p_0 \in L_+^1(0, 1). \end{cases} \quad (18)$$

where ϵ is an arbitrary small positive number. The main reason for introducing this new Problem (18) is to avoid difficulties that may come from a singularity of the arrival rate $\sigma(t)$. From Problem (7), it is possible to compute the arrival rate $\sigma(t)$ and it is given by

$$\sigma(t) = \frac{\sigma_0(t)}{1 - J \int_{1-h}^1 p(t, w) dw}.$$

Problem (18) is nothing but a mollified version of Problem (7), where the arrival rate $\sigma(t)$ is saturated in order to prevent a singularity.

We already know from [Dumont and Henry, 2012] that a such **mollified** version of the model given by (18) is globally well posed. More precisely there exists an unique p belonging to $C(\mathbb{R}_+, L_+^1(0, 1))$ solution to (18). The proof is based on the construction of a contraction mapping and the use of the Banach-Picard fixed point theorem.

Let us now assume that the initial condition p_0 belongs to X , and let us show that the solution of (18) is actually the solution of the original equation (7) at least for a short time. We have

$$1 - J \int_{1-h}^1 p_0(w) dw > 0,$$

then there exists $\epsilon_0 > 0$ such that

$$1 - J \int_{1-h}^1 p_0(w) dw > \epsilon_0.$$

Let p be the unique positive solution of the mollified Problem (18). Since p is an element of $C([0, T], L^1(0, 1))$, we deduce that the mapping

$$t \longrightarrow 1 - J \int_{1-h}^1 p(t, w) dw,$$

is continuous on $[0, T]$, which gives the existence of $\delta > 0$, such that

$$1 - J \int_{1-h}^1 p(t, w) dw > \epsilon_0, \quad \forall t \in [0, \delta].$$

It means that we have

$$S_{\epsilon_0}[\sigma](t) = \frac{\sigma_0(t)}{1 - J \int_{1-h}^1 q_1(t, w) dw}, \quad \forall t \in [0, \delta].$$

This proves that the solution p of the mollified Problem (18) is actually the solution of the original problem for all $t \leq \delta$.

We are now interested to know if the existence is global or not. In other word if the solution stays in the domain X all the time or leaves the domain producing a singularity in the value of the firing rate $r(t)$. Let us answer to this question with the following theorem.

Theorem 5 *If the parameters of the problem are chosen such that they satisfy*

$$J \geq \frac{1 - v_r}{h} + 1, \quad h\sigma_0 > \gamma, \quad (19)$$

then for all initial condition p_0 belonging to X , the solution p to Problem (7) is not a global in time solution in $C((0, T), L_+^1(0, 1))$. Furthermore the maximal time t^ for which the solution exists verifies*

$$t^* \leq \frac{1}{h\sigma_0 - \gamma}, \quad (20)$$

and the firing rate $r(t)$ blows up in the sense that

$$\limsup_{t \rightarrow t^*} r(t) = +\infty. \quad (21)$$

Before going into the proof of Theorem 5 let us give a consequence on the stationary state of Problem (7). To our knowledge, the existence of such a stationary state for the model (7) is still an open question. But one can notice that if (under the condition (19)) all initial conditions lead to a blow up in finite time, no stationary state can exist (under the same condition (19)) since if there would exist a stationary state, we would have at least one initial condition which will not blow up.

Corollary 6 *If the parameters of the problem are chosen such that they satisfy (19), then there is no stationary state to the nonlinear Problem (7).*

Nonetheless we are unable to give a result similar to Proposition 2 for a population of leaky integrate-and-fire neurons. Since the possible existence of a stationary state for (7) is still open, the study of its stability is not possible by now. Here is somehow the big lack in our attempt to generalise the results of [DeVille and Peskin, 2008] and [DeVille et al., 2010] to the leaky integrate-and-fire populations. We now prove Theorem 5.

Proof We use a mathematical technique that has been successfully used in [Cáceres et al., 2011] for the non linear noisy integrate-and-fire neuron. We work in the weak sense for Problem (7). Let p be the solution to Problem (7), then for every continuous function ϕ , we have

$$\begin{aligned} \frac{d}{dt} \int_0^1 p(t, v) \phi(v) dv + \gamma \int_0^1 v p(t, v) \frac{d}{dv} \phi(v) dv + \sigma(t) \int_0^1 p(t, v) (\phi(v) - \phi(v+h)) dv \\ + \sigma(t) \int_{1-h}^1 p(t, v) \phi(v+h) dv = \phi(v_r) r(t). \end{aligned}$$

Let us choose the special test function ϕ as

$$\phi(v) = e^{\mu v},$$

then we get that

$$\begin{aligned} \frac{d}{dt} \int_0^1 p(t, v) \phi(v) dv = -\gamma \mu \int_0^1 v p(t, v) \phi(v) dv - (1 - e^{\mu h}) \sigma(t) \int_0^1 p(t, v) \phi(v) dv \\ - \sigma(t) \int_{1-h}^1 p(t, v) \phi(v+h) dv + \phi(v_r) r(t), \end{aligned}$$

which implies

$$\begin{aligned} \frac{d}{dt} \int_0^1 p(t, v) \phi(v) dv \geq -\gamma \mu \int_0^1 p(t, v) \phi(v) dv - (1 - e^{\mu h}) \sigma(t) \int_0^1 p(t, v) \phi(v) dv \\ + r(t) (\phi(v_r) - \phi(1+h)). \end{aligned}$$

For the sake of clarity, let us introduce the new notation

$$\mathcal{M}_\mu(t) = \int_0^1 p(t, v) \phi(v) dv, \quad \alpha = \frac{\phi(1+h) - \phi(v_r)}{\mu}.$$

We get that

$$\frac{d}{dt} \mathcal{M}_\mu(t) \geq -\gamma \mu \mathcal{M}_\mu(t) - (1 - e^{\mu h}) \sigma(t) \mathcal{M}_\mu(t) - r(t) \mu \alpha,$$

and using the fact that

$$\sigma(t) = \sigma_0 + J r(t),$$

we arrive to

$$\frac{d}{dt} \mathcal{M}_\mu(t) \geq ((e^{\mu h} - 1) \sigma_0 - \gamma \mu) \mathcal{M}_\mu(t) + J(e^{\mu h} - 1) \mathcal{M}_\mu(t) r(t) - r(t) \mu \alpha.$$

Assuming that $h \sigma_0 > \gamma$ and $\mu > 0$, we have that

$$(e^{\mu h} - 1) \sigma_0 - \gamma \mu > 0,$$

which implies that

$$\frac{d}{dt} \mathcal{M}_\mu(t) \geq J(e^{\mu h} - 1) \mathcal{M}_\mu(t) r(t) - r(t) \mu \alpha.$$

Using the fact that

$$(e^{\mu h} - 1) \geq \mu h, \quad \forall \mu > 0,$$

we arrive to

$$\frac{d}{dt} \mathcal{M}_\mu(t) \geq \mu r(t) (J h \mathcal{M}_\mu(t) - \alpha).$$

Let us for the moment assume that $\mathcal{M}_\mu(0)$ satisfies the following condition

$$J h \mathcal{M}_\mu(0) \geq \alpha. \tag{22}$$

Since $r(t)$ is a positive function, we get

$$\frac{d}{dt} \mathcal{M}_\mu(t) \geq ((e^{\mu h} - 1) \sigma_0 - \gamma \mu) \mathcal{M}_\mu(t),$$

and applying Gronwall inequality we arrive to

$$\mathcal{M}_\mu(t) \geq e^{((e^{\mu h} - 1) \sigma_0 - \gamma \mu) t} \mathcal{M}_\mu(0). \tag{23}$$

On the other hand, using (5) we must satisfy the inequality

$$\mathcal{M}_\mu(t) = \int_0^1 p(t, v) \phi(v) dv \leq e^\mu, \quad (24)$$

which leads to a contradiction.

Let us now look at the assumption on $\mathcal{M}_\mu(0)$ given by the inequality (22), which is equivalent to

$$\int_0^1 p_0(v) \phi(v) dv \geq \frac{e^{\mu(1+h)} - e^{\mu v_r}}{\mu J h}.$$

Let us first notice that

$$\int_0^1 p_0(v) \phi(v) dv \geq 1,$$

then the condition (22) is implied by

$$J \geq \frac{e^{\mu(1+h)} - e^{\mu v_r}}{\mu h}.$$

One can show that the minimum value of the fonction

$$\mu \longrightarrow \frac{e^{\mu(1+h)} - e^{\mu v_r}}{\mu h}, \quad \mu > 0,$$

is in $\mu = 0$, which leads to the computation of

$$\lim_{\mu \rightarrow 0} \frac{e^{\mu(1+h)} - e^{\mu v_r}}{\mu h},$$

and using L'Hôpital's rule, we find that

$$\lim_{\mu \rightarrow 0} \frac{e^{\mu(1+h)} - e^{\mu v_r}}{\mu h} = \frac{1 + h - v_r}{h},$$

which gives us the sufficient condition (19). Let us denote by t^* the first moment when the contradiction occurs. From (23) and (24) we have that

$$t^* \leq \frac{\mu}{(e^{\mu h} - 1)\sigma_0 - \gamma\mu}, \quad \forall \mu > 0.$$

One can show easily that the minimum value of the function

$$\mu \longrightarrow \frac{\mu}{(e^{\mu h} - 1)\sigma_0 - \gamma\mu}, \quad \mu > 0,$$

is in $\mu = 0$, which gives us using L'Hôpital's rule

$$t^* \leq \lim_{\mu \rightarrow 0} \frac{\mu}{(e^{\mu h} - 1)\sigma_0 - \gamma\mu} = \frac{1}{h\sigma_0 - \gamma}.$$

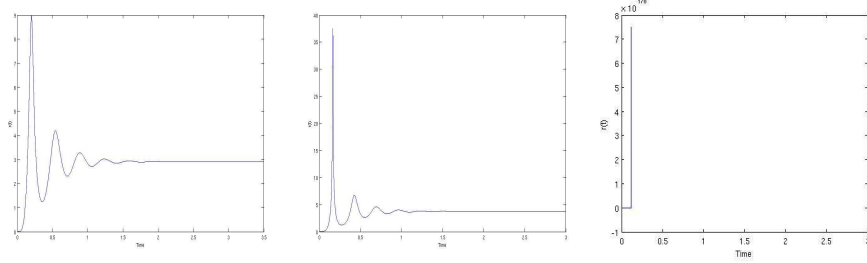


Figure 6: Simulation of the nonlinear PDE (7), in all plots, we show the evolution in time of the activity of the population $r(t)$. A gaussian function was taken as initial condition p_0 , the external influence $\sigma_0(t)$ was taken constant $\sigma_0 = 50$; potential jump size $h = 0.05$; leakage coefficient $\gamma = 1$; reset potential $v_r = 0.1$. In the first plot, the coupling parameter $J = 5$, in the second one $J = 10$, in the third one $J = 20$. We can see that the activity of the population converges to an equilibrium in the first two plots, and blows up to infinity in the third plot.

To show the blow up of the activity (21) we first notice that

$$\liminf_{t \rightarrow t^*} 1 - \int_{1-h}^1 p(t, w) dw = 0,$$

because otherwise this quantity would be bounded by below in a neighbourhood of t . Then by continuity, $p(t^*)$ would exist and p could be prolonged for $t > t^*$ in contradiction with the definition of t^* .

We present in Figure 6 some numerical results that illustrate the consequences of Theorem 5. We show the evolution in time of the activity of the population $r(t)$ for different values of the average number of connections J per neuron. In the first and the second plot of Figure 6 the activity, after oscillating, converges toward a stationary state, which means that all the neurons of the population fire in an asynchronous way. In the third plot of Figure 6 the firing rate blows up to infinity before the simulation breaks down. As it has been proposed in [DeVillle et al., 2010], we can relate the blow up of the activity to the occurrence of a Dirac mass in the firing rate, which means that a part of the population fire in the same instant. This interpretation will be discussed with more details in the last part of the paper where some fully stochastic simulations of a population of integrate-and-fire neurons are performed.

4 Stochastic simulation

In this part, we propose some simulations of a fully stochastic neural population in order to illustrate our theoretical result obtained in the previous section.

Each neuron of the population is assumed to follow the leaky integrate-and-fire model given by (1) and to be stochastically driven by an independent Poisson spike train with a constant rate σ_0 . In other words, during a short interval of time Δt , the probability that a neuron receives an impulse coming from an external source is given by $\Delta t \sigma_0$.

When a neuron fires and emits an action potential, each other neuron of the network may receive it. The action potential will cross the synapse and reach the post-synaptic neuron with a certain probability ρ , the synaptic transmission probability. In other words we consider an all-to-all coupled neural network with synaptic failure. Since the coupling parameter J of the deterministic model (7) is the average connection per neuron, it is related to the synaptic transmission probability by

$$J = \rho N,$$

where N is the total number of neurons of the considered population (see [DeVille et al., 2010] for more details). We show in Figure 7 numerical results for different values of the synaptic transmission probability ρ .

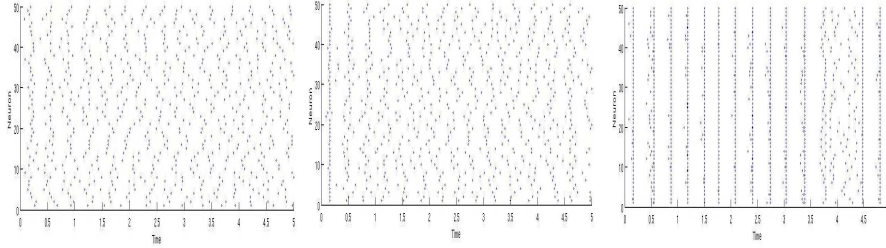


Figure 7: Simulation of a fully stochastic population of 50 integrate-and-fire neurons. At each moment a neuron fires, a blue circle is drawn in front of the corresponding firing neuron. Each neuron of the population has an initial potential that was chosen randomly following the gaussian probability, the external influence $\sigma_0(t)$ was taken constant $\sigma_0 = 50$; potential jump size $h = 0.05$; leakage coefficient $\gamma = 1$; reset potential $v_r = 0.1$. The coupling between neurons is assumed to be all-to-all with a synaptic transmission probability which is set to 0.1 in the first simulation, 0.25 in the second one and 0.4 in the third one.

For each simulation we give the raster plot of the network (see Figure 7). The raster plot is a more informative output than the firing rate since it gives the moment of firing for each neuron of the network.

The parameters of the three simulations presented in Figure 7 have been chosen to permit comparison with the simulations done with the deterministic model (7) in Figure 6. In the first two plots of Figure 7, the neurons fire in an asynchronous way with a firing rate similar to the one in the first plots of Figure 6 where the firing rate reaches a stationary level. As we can see it in the third plot of Figure 7, when the probability ρ is large enough a burst in the activity appears. Some neurons of the network fire at the exact same moment.

Similar simulations to that of Figure 7 can be found [Newhall et al., 2010a] and [Newhall et al., 2010b], where a theoretical result has been obtained to see the whole neural network firing at the same time.

The simulations of Figure 7 are consistent with our theoretical result saying that for a large enough average connection per neuron, the activity blows up, and a Dirac mass might be observed. If the simulations of the deterministic model (7) breaks down (see Figure 7) when a synchronisation of neurons takes place, the stochastic simulation can be continued after the first burst. Since the parameters are chosen such that all initial condition must blow up in finite time, after the first burst occurs the new distribution of neurons gives a new initial condition that must again blow up finite time. This phenomenon is repeated and then synchronisation of neurons appears as we see it in the last plot of Figure 7.

5 Conclusion

In this paper we have studied the model based on a population density approach that has been introduced in [Omurtag et al., 2000] to facilitate the simulation of a large population of integrate-and-fire neurons. We have made a link between this model and the recent model introduced in [DeVille and Peskin, 2008] and [DeVille et al., 2010]. It turns out that the dynamical system given by (11) and used in [DeVille et al., 2010] to explain the synchronisation property of an excitatory neural network can be seen as a particular case of the model (7).

One of the most important results established in [DeVille and Peskin, 2008] and [DeVille et al., 2010] is that for a strong connectivity between neurons, the dynamical system given by (11) does not admit a stationary solution and its solution blows up in finite time (see Proposition 1 and Proposition 2). The blow up of the solution has been related to the occurrence of a Dirac mass in the activity due to a part of the population firing at the same time. Furthermore, an estimate on the average connection per neuron J has been given to ensure the occurrence of the blow up. In this paper, using a different method we have been able to recover the same type of condition on the average connection per neuron (see Theorem 5) to get a burst for the model introduced in [Omurtag et al., 2000]. Furthermore, we have illustrated the theoretical result and its consequences by showing simulations of the deterministic model (7) in Figure 6 and simulations of a fully stochastic network of integrate-and-fire neurons in Figure 7.

Let us notice that Model (7), although it has been introduced to facilitate the simulation of large populations of neurons, can not be run if the population is strongly connected. This is due to the blow up of the solution in finite time and a map that models the discontinuity after the blow up should be necessary to pursue the simulation.

Another important result that has been proved in [DeVille and Peskin, 2008] and [DeVille et al., 2010] is the existence and stability of the stationary state for a weakly coupled population, and its non existence for a strongly connected

population (see the Corollary 6). Unfortunately we failed in proving the existence of a stationary state for Problem (7) in the weakly connected case. We then could not investigate its stability. In the future, it seems to us really interesting to show that for a constant external stimulation with parameter $\sigma_0(t) = \sigma_0$ and a weak connectivity between neurons there exists a unique stationary state. In the simulation (cf. Figure 5 and see also [Sirovich et al., 2000] and [Knight et al., 2000]), the density function converges asymptotically to a stationary state. Since it corresponds to an asynchronous state of the neural network, its nonlinear analysis has a big interest.

Another important work to do is to investigate the role of the delay in the model. Two types of delay can be added, one that takes into account the refractory period of a single cell and one for the synaptic time that has been neglected in this paper. As we already know from [Dumont and Henry, 2012], adding delay in the feedback of the activity (a synaptic time) prevents the blow up of the solution. Bursts where all the population or a part of it fires at the same time do not happen and the exact synchronisation disappears nevertheless narrow peaks in the activity remain for small delays. It should be interesting to clarify the occurrence of periodical solutions in this case. This will be a new topic of investigation.

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